Plant-bee interactions within pollinator habitats embedded in eastern Nebraska agroecosystems

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Abstract - In the Great Plains region of the United States, land use change continues to negatively affect wild bee communities by limiting the availability of food and nesting resources. Concurrently, there is limited research describing bee species preferences for flowering plant species, including seasonal preferences. We monitored and surveyed previously established pollinator habitats in eastern Nebraska throughout the growing season for 2 years to assess bee-plant interactions of both honey bees and wild bee species. We observed seasonal variability in forbs where abundance and species richness were generally higher in the early and mid-seasons, but we did not observe seasonal differences in bee abundance or bee species richness. We used a resource use metric to highlight plant species used by wild bees and honey bees throughout the growing season. Forb species utilization varied by bee group, where wild bees most preferred *Oligoneuron rigidum* (L.) Small (Stiff goldenrod), *Helianthus annuus* L. (Annual sunflower), and *Ratibida pinnata* (Vent.) Barnh. (Grey-headed coneflower), while honey bees preferred *Asclepias syriaca* L. (Common milkweed), *Polygonum pensylvanicum* L. (Pennsylvania smartweed), and Annual sunflower. Our observations of plant-pollinator associations indicated minimal resource use overlap between honey bees and wild bees. Three bee species of conservation concern were encountered during our transects, including *Megachile rugifrons* Smith (Rugose-fronted resin bee), *Bombus fraternus* Smith (Southern Plains bumble bee), and *B. pensylvanicus* De Geer (American bumble bee). This study provides insight into the seasonal utilization of resources occurring among bee species within established pollinator habitats in eastern Nebraska. These findings will assist in improving and refining pollinator habitat seed mix designs to provide high quality, season-long, pollinator habitats within Midwestern working landscapes.

Introduction

There is growing evidence documenting declines in populations of bee species, including in relation to anthropogenically generated land use change and habitat fragmentation (Cariveau and Winfree 2015, Kammerer et al. 2021, Otto et al. 2016). Among agricultural habitats, the degradation, conversion, and fragmentation of natural and semi-natural habitat (Kremen et al. 2002, Richards 2001) via loss of flower-rich landscapes (e.g. Goulson et al. 2008) negatively affects abundance and richness of bee species (Winfree et al. 2009).

In the United States, approximately 17% of the land base is in crop production (Bigelow and Borchers 2017) and numerous crops benefit, and are benefited by, wild bee pollination (Losey and Vaughan 2006; Kremen 2008). However, fragmented and isolated habitats, such as those that occur within many agricultural systems, are associated with decreased pollinator abundance, species richness and functional diversity when compared to intact natural and semi-natural lands (Evans et al. 2018, Ewers et al. 2006, Vickruck et al. 2019). Declining pollinator abundance and diversity can negatively impact plant reproductive success by reducing seed set potential (Steffan-Dewenter and Tscharntke 1999) even as agricultural crops located near natural and semi-natural areas may achieve higher crop yields (Kremen

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et al. 2002, 2004; Mallinger et al. 2019a; Winfree et al. 2007). These findings highlight that agroecosystems are vital to addressing bee declines and that less fragmented landscapes, containing intact pollinator habitat, have great potential to benefit both wild bee populations and agricultural productivity.

Pollinator habitat establishment among agroecosystems typically includes non-crop herbaceous buffer strips around and between fields, roadside plantings and management, and seeding of habitat on low-productivity and non-farmable private parcels (Decourtye et al. 2010, Haaland et al. 2011, Wratten et al. 2012). Maintenance of hedgerows, trees, and shrubs around fields can serve as fire and wind breaks, pesticide drift barriers, and refuge for woodland edge species (Boutin and Jobin 1998, Corbit et al. 1999, Morandin and Kremen 2013a,b). Within fields, the planting of cover crops that provide pollinator resources within farmable fields (Altieri 1999, Mallinger et al. 2019b), has been shown to add increased value to agricultural landscapes.

There is increasing awareness and urgency to understand local plant-pollinator interactions so that pollinator-utilized seed mixes can be selected to maximize their potential benefits. In relation to plants that support pollinators, the terms "beneficial" and "recommended" are generally understood to relate to forbs on which bees are observed. A resource may be considered preferred when it receives more visitation than would be expected relative to its abundance (Bartomeus et al. 2016, Simanonok et al. 2021). Not only are understanding bee utilization and preference of forbs critical for provisioning effective habitat, but they are also critical in elucidating changes in seasonal forage preferences in temperate climates (Simanonok et al. 2021). In such climates, both wild bee and plant phenology change through time, and many adult bee life stages are linked to those of their preferred host plants (Bendel et al. 2019, Wood et al. 2018). Research is needed to inform conservation plans and habitat designs based on field-derived data that account for known shifts in plant and bee phenology, providing plants utilized by wild bees over the entire growing season (Vaudo et al. 2015, Williams and Lonsdorf 2018).

The Midwestern U.S. is a critical region for studying and supporting bees and other pollinators (Hellerstein et al. 2017; Koh et al. 2016; Otto et al. 2016, 2018). Nebraska is home to roughly 400 wild bee species with diverse life history traits and varied susceptibility to environmental stressors (Ascher and Pickering 2020). The state has experienced substantial land use change over time, including grassland habitat loss and conversion due to the intensification of row crop agriculture and infrastructure (Otto et al. 2016, Wright et al. 2017, Wright and Wimberly 2013). The larger region also serves as a summer foraging ground for nearly one-third of all commercial, honey-producing and pollinating honey bee colonies in the U.S. (e.g. USDA-NASS 2020), and is home to several bumble bee species that are endangered or of conservation concern, including *Bombus affinis* Cresson (Rusty-patched bumble bee), *Bombus fraternus* Smith (Southern plains bumble bee), *Bombus pensylvanicus* De Geer (American bumble bee), *Bombus occidentalis* Greene (Western bumble bee), and *Bombus fervidus* Fabricius (Yellow bumble bee) (Grixti et al. 2009, Lamke et al. 2022, Rosenberger and Conforti 2020). Despite the significance of Midwestern U.S. natural and semi-natural habitats to support bee species and many other wildlife taxa, the region has continued to experience substantial land use change over time, resulting in losses of suitable bee habitat across the region (Hellerstein et al. 2017, Koh et al. 2016, Otto et al. 2016).

For this study, we conducted seasonal bee biodiversity and floristic surveys among pollinator habitat patches located within agricultural landscapes of eastern Nebraska to,

1) Describe seasonal and interannual forb abundance and species richness,
2) Describe seasonal and interannual bee abundance and species richness,

3) Illustrate seasonal foraging patterns of honey bees and wild bee species, and
4) Derive relative forb utilization preferences by honey bees and wild bees.

Methods

2.1 Study locations

During the springs of 2021 and 2022, private lands providing a variety of pollinator habitat types, including the Bee and Butterfly Habitat Fund (BBHF, *n* = 8, www.beeandbutterflyfund.org/), Conservation Reserve Program (CRP, practice CP-42 (Pollinator Habitat, *n* = 4, www.fsa.usda.gov/programs-and-services/conservation-programs/crp-practices-library/index), an expired CRP field (*n* = 1)), or having seeded the Stock Seed Pollinator Mix (SSPM, *n* = 1, www.stockseed.com/Shop/wildflower-mixtures/stock-s-pollinator-mixture) were identified and selected based on the following criteria: 1) enrolled habitat size greater than 1.2 hectares (3 acres), 2) habitat age 3-5 years post planting, and 3) located in eastern Nebraska. The BBHF (St. Paul, NE) provides landowners with pollinator seed mixes and technical assistance for project establishment and management. Stock Seed Farms, located in Murdock, NE, is a local vendor growing and selling native grass and forb seed mixes to private landowners and also mixing seed for national USDA conservation programs. A total of 10 counties were represented among the 14 distinct sites in the final selection. The distance between any two sites ranged from 9.18 km – 185.18 km, well outside the typical flight range for bees. Surveys occurred at the 14 sites across two years (10 sites in 2021 and 9 sites in 2022), wherein we visited each site three times per growing season. Sites C, I, L, M, and N were surveyed in both years, while sites B, D, E, G, and J were dropped for the 2022 study year in exchange for sites A, F, H, and K. Exchanging one site for another between years occurred for a variety of reasons such as an inability to contact landowners during the subsequent year, change in land ownership, change in land use, or due to excessive travel distance.

2.2 Plant-bee Surveys

Plant-bee interaction data were collected at each site along transects measuring 2m in width by 20m in length. Three such transects were conducted during each study site visit. As such, we considered a transect to be a single 2x20m plant-bee survey wherein the species identification and number of stems of all blooming forbs were recorded along with any associated bee visitations (during a 10-minute search period) to those plant species. As flowering plants tended to occur in a patchy and sometimes sparse distribution, transect starting points and directions were selected semi-randomly to ensure encounter of actively blooming plants within each site. Upon arriving at a site, surveyors first visually assessed whole-site flowering plant abundance and richness and subsequently transect starting points were determined to maximize plant abundance and richness encounter rate. Surveys occurred three times per growing season, spaced approximately five weeks apart, during the expected peak bloom periods in each primary sub-season; early (June 8th-23rd), mid (July 20th-28th), and late (August 31st- September 10th) seasons. In total, 57 total site visits were completed, amounting to 171 transects (at three transects per site per visit) across the two years of the study.

Actively blooming flowers were identified to species in the field using the iNaturalist/SEEK app, wildflower field guides (Newcomb 1989, Peterson and McKenny 1975), and by examination of site-level seed mix lists. We conducted transects when ambient temperatures were greater than 15.5° C, wind speeds were less than 18 kilometers per hour, relative humidity was between 30-72%, and under a variety of cloud covers, ranging from overcast to clear skies. Surveys were conducted between the hours of 0900 – 1600.

A flowering stem was defined by the point at which the stem, containing at least one actively blooming flower, met the soil regardless of the number of floral heads or inflorescences present on the stem. Due to variation in seed mix design from program designators, some species were intentionally seeded at some sites, while the same species may have been wild or considered volunteer at other sites. Therefore, observed blooming plants were cross-referenced with seed mix lists for each site to determine whether they were seeded or volunteer species. The Lady Bird Johnson Wildflower Center Database (wildflower.org) and the USDA Plants database (USDA NRCS 2023) were used to standardize scientific and common names, growth frequency, and indigenous status relative to the United States.

Along each transect, bee sampling was accomplished by employing 3 standard techniques during 10-minute timed searches: 1) aerial sweep nets were used over dense patches of a flower species (e.g. Alfalfa and vetches), or particularly tall and hard to reach flowers (e.g. sunflower, cup plant), 2) 50 ml falcon tubes were used to collect foraging bees on all other individual flowers, and 3) visual observations were used to record flower visits by *Apis mellifera* L. (Western honey bee) and *Bombus* spp. (bumble bee) queens, (i.e., no *A. mellifera* or *Bombus* queens were collected in this study). Wild bees were only captured when they were observed on flowers, presumably foraging for nectar or pollen. Wild bee specimens were pinned and identified at the University of Nebraska-Lincoln Bee Lab by S. Lindsay utilizing dichotomous keys (Arduser 2022, Ascher and Pickering 2020, Michener 2007, Michener et al. 1994). Physical voucher specimens for all encountered wild bee species are housed at the University of Nebraska-Lincoln's Nebraska Hall and all databased records, including all bees collected and their floral associations, are available via SCAN (https://scan-bugs.org/portal/, Collection: UNSMe).

2.3 Analysis

All analyses were conducted using R version 4.2.2 (R Core Team 2022). Individual transects ($n = 3$ per site visit) were used as replications of each field site within each season (early, mid, and late) and year. Flowering plant stem abundance per transect was determined as the mean number of flowering stems of all plant species observed among the 3 transects occurring at each site during each seasonal ($n = 3$) sampling event per year. Similarly, bee abundance (as bees per transect) was determined as the mean number of bees among the 3 transects occurring at each site during each seasonal ($n = 3$) sampling event per year. Likewise, species richness (both plants and bees) was determined as the mean number of species observed among the three transects occurring at each site during each seasonal ($n = 3$) sampling event per year.

Flowering plant stem abundance, bee abundance, and bee species richness were each used as response variables in linear mixed effect modeling (lme4 package) to examine fixed (season and year) and random (site) effects in the study. Count data for both bees and plants were log-transformed to normalize their distributions prior to statistical analyses. To illustrate interactions between plants and bees, bipartite alluvial plots were created using R packages ggplot2 and ggalluvial (R Core Team 2022). Bipartite alluvial plots were created seasonally for the top 20 interactions between plants and bees.

A floral preference index (i.e. resource use index) was used (Johnson 1980; Williams et al. 2011) wherein all forb species with $n > 1$ observed bee visit and $n > 20$ total stems counted (summed among all seasons and years) were ranked (1-n) relative to their number of bee visits. Forbs were also ranked from highest to lowest number of blooming stems observed (1-*n*, summed among all seasons and sampling years). The floral preference index was derived as the difference between the bee visitation rank and the stem abundance rank, where a greater difference indicated greater preference for a given forb by bees (wild and honey bee preference indices were each generated separately). Tied rank differences were allowed to occur and were left as such.

Results

3.1 Forbs

A total of 101 species of flowering forbs were observed over the two-year study, totaling 47,207 blooming stems among all sites, transects, seasons, and years. The number of blooming stems per species on an individual transect ranged from 1 ($n = 50$ species in the dataset) to 1500 (*Medicago sativa* L., Alfalfa). The sum number of stems per individual site ranged from 116 to 4529, while plant species richness ranged from 2 to 21 species (SI Table 1). There was a significant positive correlation ($t_{58} = 3.21$, $r = 0.39$, $p = 0.002$) between flowering plant stem abundance and flowering plant species richness among all sites, seasons, and years, meaning that as the abundance of flowering plant stems increased in a sample (site by season by year) so too did the species richness within that sample (SI Figure 1).

We observed a significant interaction between season and year relative to forb stem abundance ($F_{2,54} = 3.14$, $p = 0.05$) where the early and mid-season surveys in 2021 had higher stem abundances compared to those conducted in the late season, but stem abundance did not significantly vary among seasons in 2022 (Figure 1a). Forb stem abundance did not vary ($F_{2,57} = 0.79$, $p = 0.46$) across the three conservation programs we evaluated: BBHF, CRP, and SSPM.

Plant species richness varied by season ($F_{2,44} = 7.23$, $p = 0.002$) where the mid- and late seasons were statistically different, and year ($F_{1,54 =}$ 18.68, $p < 0.0001$) (Figure 1b). We did not observe a statistically significant interaction between season and year. Further, plant species richness did not vary across BBHF, CRP and SSPM ($F_{2,57} = 1.13$, $p = 0.33$).

Within each year, stem abundance and species richness through time varied among sites (Figure 2). The highest number of blooming plant stems per transect among sites, seasons, and years occurred in the early season of 2021 at site N (CRP-CP42), sites C and E (BBHF), and again in the mid-season of 2021 at site C (Figure 2). The lowest plant stem abundances occurred in the late season of 2021 (site I: BBHF), mid-season of 2022 (site M: retired CRP), and late season of 2022 (site H: BBHF, site K: CRP-CP42). The highest plant species richness observed among sites, seasons, and years occurred in the mid-season of 2021, including at sites B and C (BBHF) and site K (CRP-CP42). Flowering plant species richness was lowest in the early (site F: CRP-CP42, site I: BBHF) and late (site H: BBHF) seasons of 2022 (Figure 2).

Of all plant species encountered throughout the study ($n = 101$), 73.2% were perennial species ($n = 74$), 10.9% were biennial species ($n = 11$), and 15.8% were annuals ($n = 16$) (SI Table 2). Most species (69.3%, $n = 70$) were native to Nebraska (USDA NRCS 2023, wildflower.org). Sixty-two percent of the blooming plants encountered were intentionally seeded in the given site's habitat. Thirty-one percent of plants encountered were volunteer species which included a mix of native volunteers and non-native weeds such as thistles (SI Table 2). The few remaining plants could not be verified due to the absence of a seed mix list (at site M) which was a retired CRP field that remained fallow and consisted of seeded wildflowers and other volunteer species.

Four plant species had a 100% establishment rate (i.e. they were detected at every site where they occurred in a seed mix): Annual sunflower, *Silphium integrifolium* Michx. (Entire-leaved rosinweed), *Melilotus officinalis* (L.) Lam. (Yellow sweet clover), and *Prunella vulgaris* L. (Self-heal). There were five more plant species that had > 80% establishment rate: including *Ratibida pinnata* (Vent.) Barnh. (Grey-headed coneflower), *Heliopsis helianthoides* (L.) Sweet (False sunflower), *Trifolium pratense* L. (Red clover), *Solidago canadensis* L. (Canada goldenrod), and *Achillea millefolium* L. (Common yarrow). Fifteen additional plant species were observed on 50-79% of sites where they were seeded, while 24 species were observed on < 50% of sites where they were seeded, but at least once (SI Table 2). Among the 14 sites and two years of the study, an average of 33% of the plants originally seeded were observed blooming (min: 23% at site J, max: 63% at site N). Overall, 50 non-annual plant species (41% of all plants on a seed mix list) were seeded but not observed during our study.

3.2 Bees

A total of 1,188 individual bees were either collected ($n = 832$) or observed (honey bees, bumble bee queens, $n = 356$) during the study, representing 5 families, 27 genera, and 73 species. As with the flowering plants, we found that the abundance of bees and bee species richness were positively correlated ($t_{58} = 7.65$, $r = 0.71$, $p < 0.0001$) among all sites, seasons, and years, meaning that as the abundance of bees increased in a sample (a site by season by year) so too did the species richness within that sample (SI Figure 1). Bee abundance did not vary by season ($F_{2,56} = 1.15$, $p = 0.33$), year ($F_{1,56} = 0.18$, $p = 0.68$), or program designation

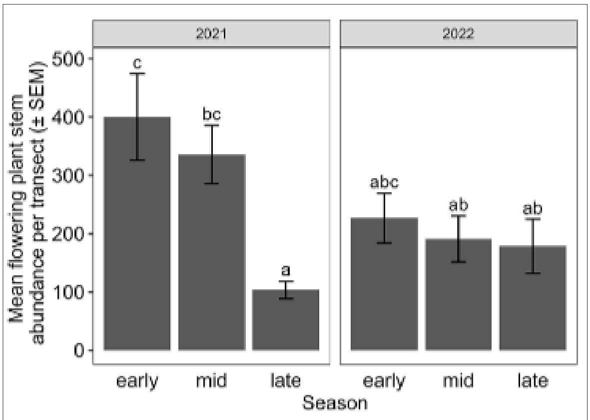

Figure 1a. Flowering plant stem abundance (mean ± SEM per transect) by season (early, mid-, late) and year (2021, 2022). Analyses were conducted on log-transformed flowering plant stem abundance, but untransformed data are depicted here for ease of interpretation. Letters denote statistically significant differences among all years and seasons (α ≤ 0.05).

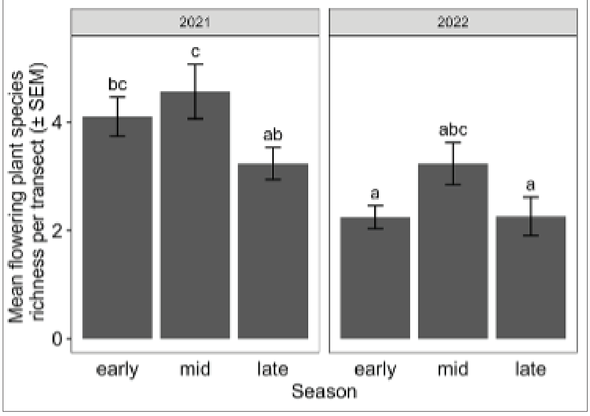

Figure 1b. Flowering plant species richness (mean ± SEM per transect) by season (early, mid-, late) and year (2021, 2022). Analyses were conducted on log-transformed stem abundance, but untransformed data are depicted here for ease of interpretation. Letters denote statistically significant differences among all years and seasons (α ≤ 0.05).

($F_{2,57} = 0.22$, $p = 0.80$). Likewise, bee species richness did not statistically vary by season ($F_{2,56} = 2.3$, $p = 0.11$), year ($F_{1,56} = 0.02$, $p = 0.89$), or program designation ($F_{2,57} = 0.19$, $p = 0.83$).

The highest bee species richness among sites by season and year occurred at site K (mean = 14 species, CRP-CP42) in the late season of 2022, site G (mean = 13, BBHF) in the late season of 2021, site C (mean = 12 species, BBHF) and site M (mean = 12 species, CRP) in the mid-season of 2021, and site L (mean = 12, SSPM) in the mid-season of 2022 (Figure 3). The lowest bee species richness occurred at site L (mean = 1, SSPM) in the late season of 2021, site N (mean = 1 species, CRP) in the early season of 2022, and site B (mean = 1, BBHF) in the early season of 2021 (Figure 3).

Apidae was the most abundant (*n* = 677) and species rich (*n* = 30) family when including honey bee observational counts, representing 57% of all bees and 41% of all species observed. Halictidae was the next most abundant (*n* = 400) and species rich (*n* = 22) family,

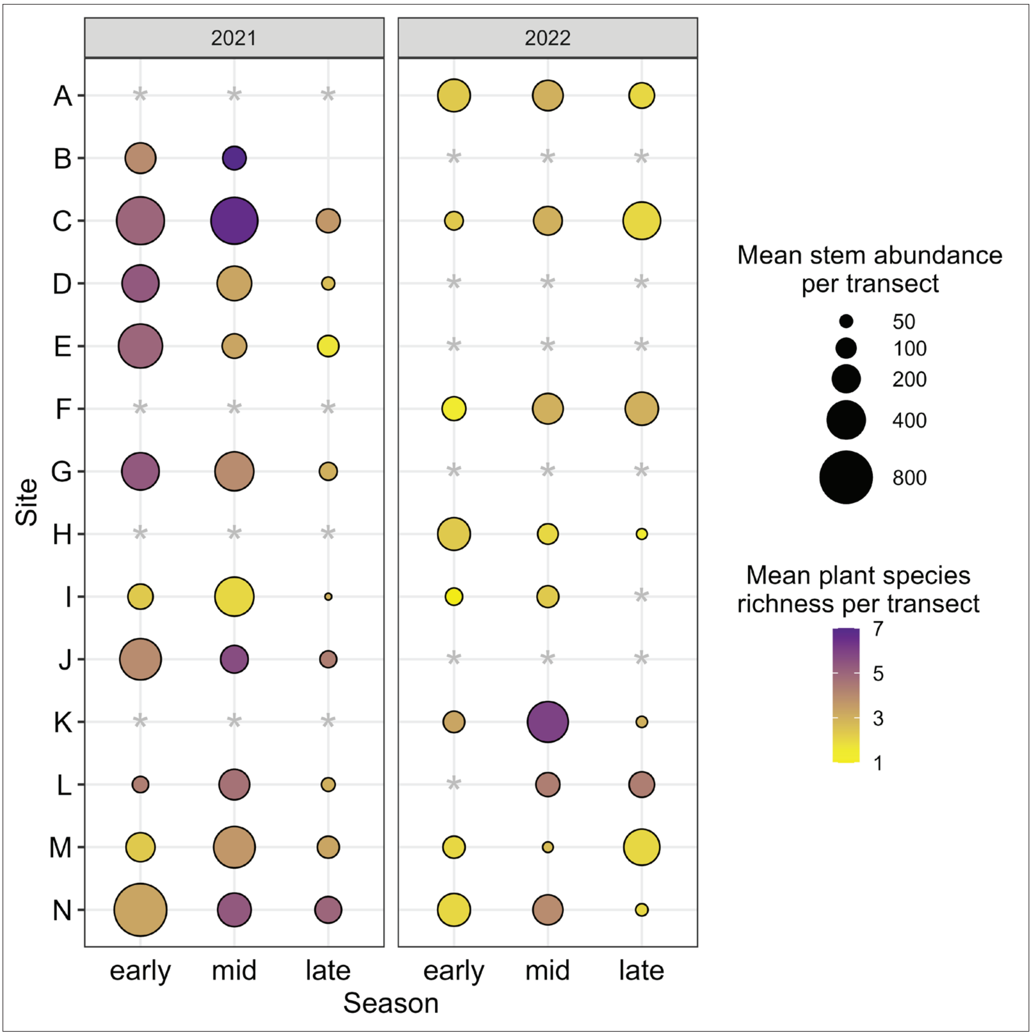

Figure 2. Plant species abundance and richness by site, season, and year. Size of circles indicates plant abundance. The color of the circles indicates species richness. Asterisks denote sites that were not sampled within a given season or year.

representing 34% of all bees. Ground nesting bees were the most common of the wild bee species collected, representing 70% of species richness and 62% of individual bees. The majority of observed bee species were solitary (70%). Over 78% of species observed were polylectic, or generalist foragers.

We encountered three wild bee species recognized as endangered or imperiled, classified by G2 or G3 conservation status (NatureServe.org). We collected a single female *Megachile rugifrons* Smith (Rugose-fronted resin bee) at site L during the mid-season on July 22nd, 2022 (SI Tables 2 and 3). At the time of collection, the bee was visiting flowers of *Eryngium yuccifolium* Michaux (Rattlesnake master). We collected 3 *B. fraternus* (Southern plains bumble bee) during both the mid- and late seasons of 2021 (1 female on *Monarda fistulosa* L. (Wild bergamot), 1 male on *Symphyotrichum novae-angliae* (L.) Nesom (New England aster) at site G) and during the late season of 2022 (1 female on *Helianthus grosseserratus* Martens (Sawtooth sunflower) at site C). Finally, we encountered 38 *B. pensylvanicus* (American bumble bee) during our surveys. Individuals were collected on 13 different plant

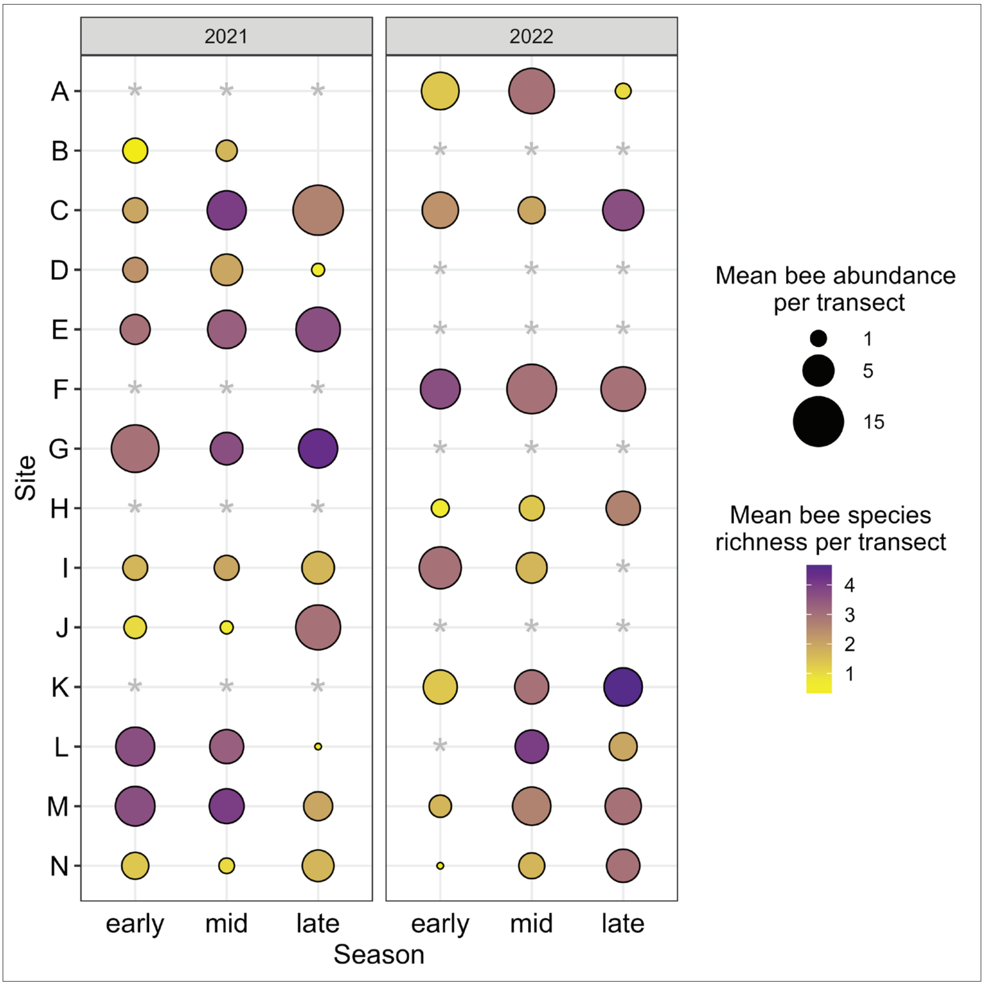

Figure 3. Bee species abundance and richness by site, season, and year. Size of circles indicates bee abundance. The color of the circles indicates species richness. Asterisks denote sites that were not sampled within a given season or year.

species (SI Tables 2 and 3) among 9 different sites in the mid- and late seasons of 2021 and 2022.

3.3 Plant-bee Interactions

While both abundance and richness of plants and bees, respectively, were positively correlated, we did not detect significant relationships between bee abundance and plant stem abundance (t_{58} = -0.91, r = -0.12, p = 0.37), bee species richness and plant stem abundance (t_{58} = -0.12, r = -0.02, p = 0.90), bee abundance and plant species richness (t_{58} = -0.89, r = -0.12, p = 0.38), or bee species richness and plant species richness (t_{58} = -0.03, r = -0.004, p = 0.98) (SI Figure 1). Of the 101 plant species observed on transects, 63 species (62%) were visited by bees. The highest number of bees per stem occurred on *Silphium laciniatum* L. (Compass plant, mean = 1.2 bees per stem), but overall bee species richness was relatively low (3 species of bees). The highest bee species richness was recorded on Canada goldenrod (21 species of bees) and on False sunflower (21 species of bees), but both had relatively low bees per stem abundance, at 0.1 and 0.02 bees per stem, respectively.

To discern seasonal community connections, we examined the top 20 plant-bee interactions that occurred within each season. Among the top 20 plant-bee interactions in the early season (Figure 4), *Penstemon digitalis* (N.) Sims (Foxglove beardtongue) had the most observed bee visitations (51 bees from 3 groups: *Bombus* spp. queens (37), *Ceratina calcarata* Robertson (Wide-legged little carpenter bee) (10), *Hylaeus mesillae* (Cockerell) (Mesilla Valley yellow-faced bee) (4)), followed by Common milkweed visited by 37 honey bees, and Yellow sweet clover observed being visited by 24 honey bees and 8 *Lasioglossum imitatum* (Walker) (Bristle sweat bee).

Among the top 20 plant-bee interactions occurring in the mid-season (Figure 5), Wild bergamot had the most observed bee visitations (97 bees from 4 groups: honey bees (45), *Bombus* spp. including queens (29), *Lasioglossum imitatum* (17)*, and Melissodes communis* Cresson (Common long-horned bee) (6)), followed by *Chamaecrista fasciculata* (Michx.) Greene (Partridge pea) visited by 26 honey bees and 5 *Bombus griseocollis* (De Geer) (Brown-belted bumble bee), and finally Prairie coneflower observed being visited by 19 *Halictus ligatus* Say (Ligated gregarious sweat bee) and 7 *Triepeolus lunatus* (Say) (Crescent-shaped cuckoo nomad bee).

In the late season (Figure 6) the top 20 plant-bee interactions included Pennsylvania smartweed which had the most observed bee visitations (79 honey bees), followed by Canada goldenrod visited by 25 honey bees, 20 *Halictus confusus* Smith (Confused sweat bee), 14 *Lasioglossum Dialictus* sp., and 9 *Augochlorella aurata* (Smith) (Golden sweat bee), and finally Stiff goldenrod observed being visited by *H. ligatus* (18)*, Lasioglossum imitatum* (9), and *Lasioglossum Dialictus* sp. (7).

Forty plant species, with greater than 20 blooming stems observed, were preferred by wild bees (Table 2, Abundance Preference > 0). Stiff goldenrod (native), Annual sunflower (native), and Grey-headed coneflower (native) ranked highest relative to wild bee abundance rank difference. There were 10 plant species that were non-preferred for supporting wild bee abundance (Table 2, Abundance Preference < 0), including Alfalfa (non-native), *Vicia villosa* Roth (Hairy vetch, non-native), and Partridge pea (native).

Thirteen plant species were considered preferred by honey bees (Table 3, Abundance Preference > 0), including Common milkweed (native), Pennsylvania smartweed (native), and Annual sunflower (native). There were 8 plants that were considered non-preferred (Table 3, Abundance Preference < 0) by honey bee, including Alfalfa, Hairy vetch, and Foxglove beardtongue (native). *Hibiscum trionum* L. (Flower-of-an-hour, non-native) ranked as preferred, however was below the threshold of 20 stems, so its preference cannot be confirmed here due to its low stem abundance among surveys.

Discussion

Due to the declines that many wild bee populations have experienced globally (Potts et al. 2010, Zattara and Aizen 2021) it is of increasing importance to incorporate research-based considerations into conservation plans and landscape designs. Therefore, it is crucial to understand seasonal flower selection by bees to maximize the effectiveness of conser-

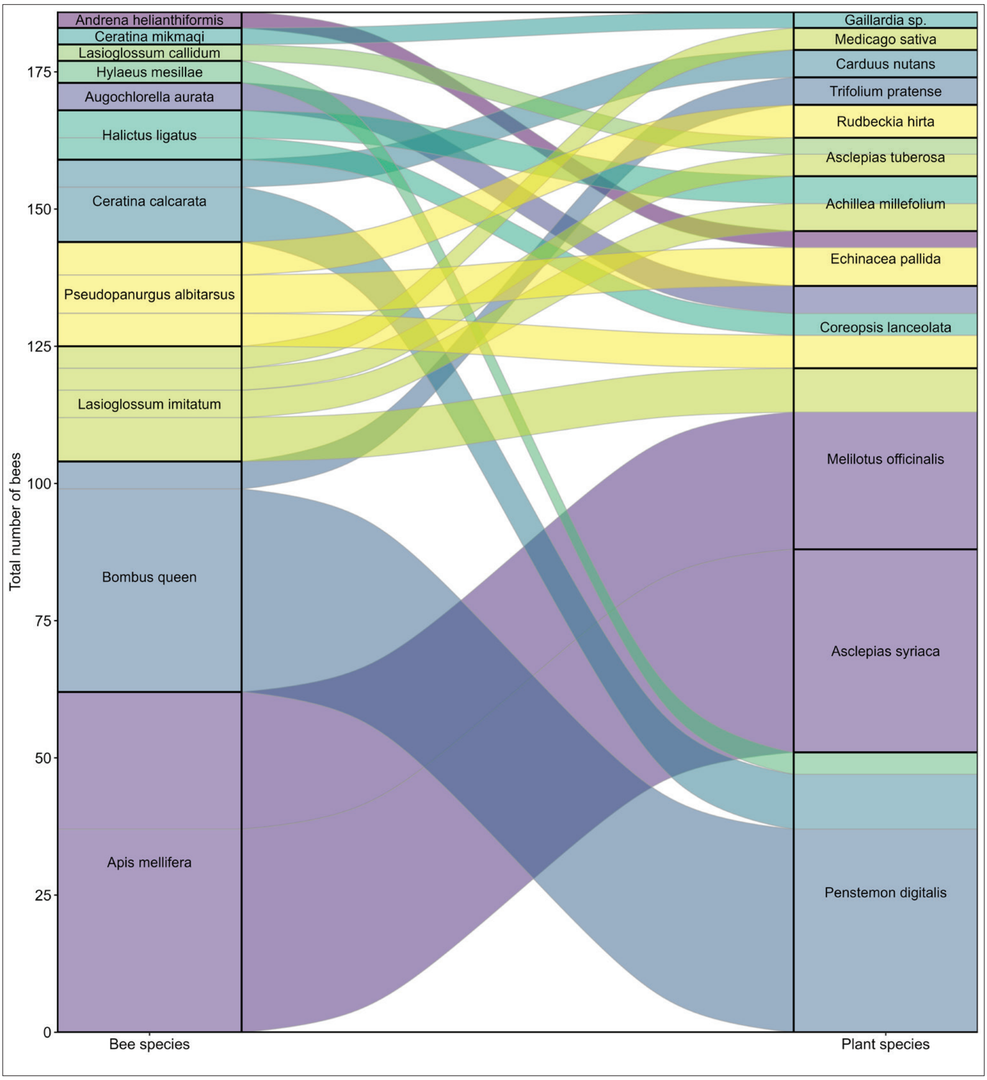

Figure 4. Bipartite alluvial plot for the top 20 bee-plant interactions in the early season among all sites and years. Bee species are listed on the left *y* axis and plant species are listed on the right *y* axis. Width of the bar on the bee *y* axis indicates total bee abundance of each bee species (numerically indicated on the left *y* axis) visiting flowers of each plant species. Each color is unique to each bee species.

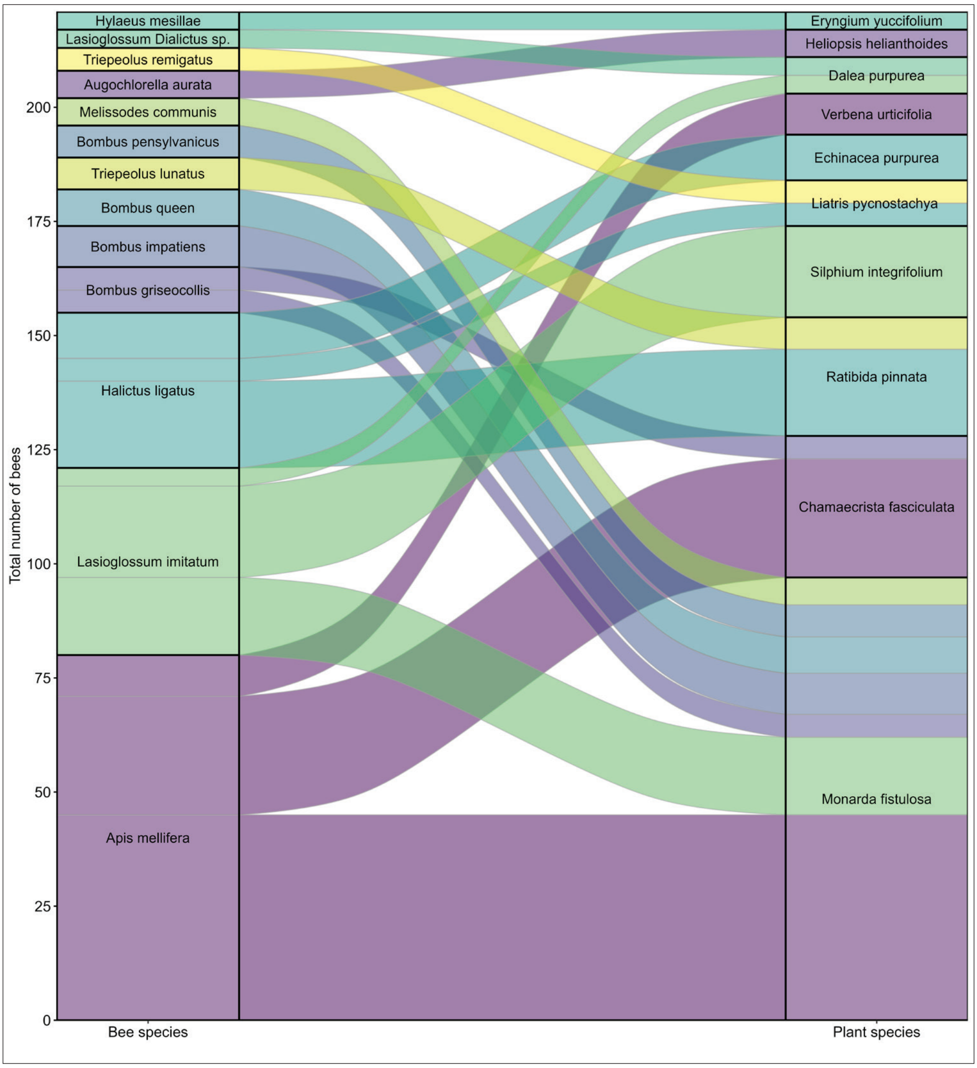

Figure 5. Bipartite alluvial plot for top 20 bee-plant interactions in the mid-season among all sites and years. Bee species are listed on the left *y* axis and plant species are listed on the right *y* axis. Width of the bar on the bee *y* axis indicates total bee abundance of each bee species (numerically indicated on the left *y* axis) visiting flowers of each plant species. Each color is unique to each bee species.

vation efforts. The results of this study document bee species richness and abundance on pollinator habitats in agricultural areas of Nebraska and highlight selection of pollinator-attractive forbs by bees throughout the growing season.

All sites surveyed represented pollinator-focused habitat establishments within agroecosystems in the tallgrass prairie (TGP) region of the United States. These sites showed a general pattern of highest forb species richness and stem abundance in the early and mid-seasons, with lower richness and abundance in the late seasons. This is consistent with other observations of plantings across the TGP region that favor mid-summer forb species in seed mixes (Delaney et al. 2015, Smart et al. 2021). The most abundant (highest number of stem counts) mid-summer species included Wild bergamot (native), Hairy vetch (introduced), Partridge pea (native), Alfalfa (introduced), and Red clover (introduced). Wild bergamot contributed substantially to bee richness and abundance in the mid-season (Figure 5) but was not calculated as a preferred resource for wild bees overall (Table 2). Seed mixes favoring mid-season bloom over the early and late seasons could result in bee-plant community mismatch, as adequate resources may be absent for initial early season nest site selection and late season nest provisioning (Thomas and Kunin 1999).

The seasonal peak in bee abundance occurred during the late season (August - September). A significant portion of this abundance was driven by honey bees (Figure 6); how-

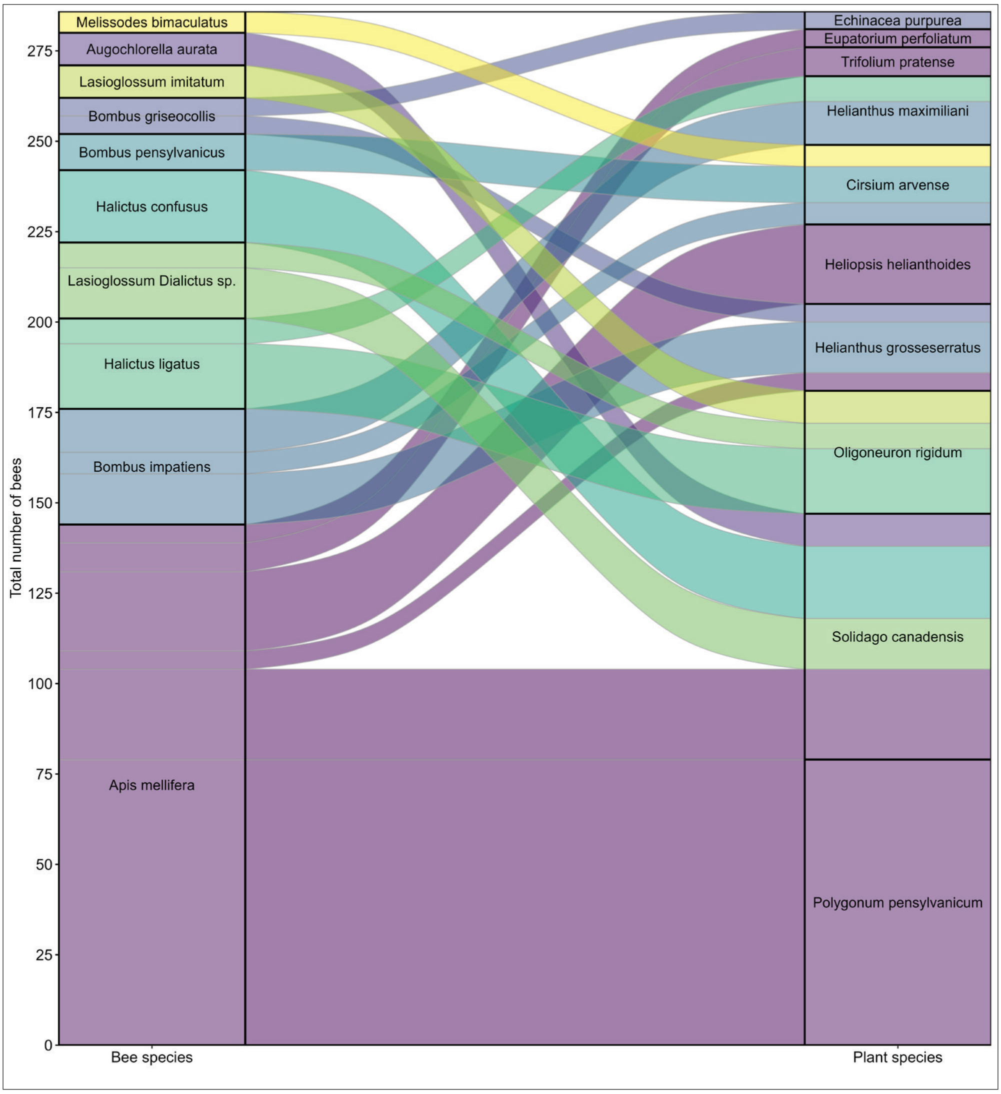

Figure 6. Bipartite alluvial plot for top 20 bee-plant interactions in the late season among all sites and years. Bee species are listed on the left *y* axis and plant species are listed on the right *y* axis. Width of the bar on the bee *y* axis indicates total bee abundance of each bee species (numerically indicated on the left *y* axis) visiting flowers of to each plant species. Each color is unique to each bee species.

Table 1. Wild bee preferences of flowering plant species with greater than 20 blooming stems. For ease of depiction, the top 10 preferred and 10 least preferred are shown. Wild bee richness is the number of bee species collected on each plant species among all sites, seasons, and years. Wild bee abundance is the number of individual bees collected on each plant species among all sites, seasons, and years. Stem abundance is the total number of stems of each plant species among all sites, seasons, and years. Stem abundance rank is the rank (1−*n*) based on stem abundance. Bee abundance rank is the ranked plant species (1−*n*) relative to the total number of wild bees collected. Wild bee abundance preference rank is the difference between stem rank and wild bee abundance rank.

Plant common name	Wild bee richness	Wild bee abundance	Wild bee abundance rank	Stem abundance	Stem abundance rank	Wild bee abundance preference rank
Stiff goldenrod	6	40	4	33	48	44
Annual sunflower	11	15	14	54	45	31
Grey-headed coneflower	3	4	23	24	50	27
Western ironweed	6	8	20	46	46	26
Canada thistle	8	31	8	168	31	23
White prairie clover	7	16	13	134	36	23
Rattlesnake master	7	11	17	92	40	23
Whorled milkweed	2	2	25	33	48	23
Chicory	1	1	26	29	49	23
Field mustard	1	2	25	41	47	22
White Dutch clover	5	7	21	625	17	−4
Purple crown-vetch	5	10	18	840	13	−5
Red clover	9	15	14	1902	8	−6
White vervain	3	4	23	658	16	−7
Yarrow	8	17	12	3208	4	−8
Yellow sweet clover	7	15	14	2254	6	−8
Upright coneflower	7	7	21	1105	10	−11
Partridge pea	9	14	15	3521	3	−12
Hairy vetch	4	9	19	3010	5	−14
Alfalfa	10	13	16	9325	1	−15

ever, *Bombus* and halictid species were also abundant during this time and continued to be through the mid- and late seasons. This peak in abundance is likely driven by the continuous growth of honey bee and bumble bee colonies through the growing season and the final generation emergence in the late summer at which time new bumble bee foundresses and males emerge to mate (Oertli et al. 2005).

The turnover of bee species over the duration of the summer is due to specific life histories that vary by species. The activity periods of wild bees are limited to only a few weeks or even days in some species (i.e. *Andrena* spp.) (Danforth et al. 2019, Michener 2007), while others may exhibit frequent activity for months (e.g. *H. ligatus, Bombus* spp.). For example, Minckley et al. (1999) reported a median similarity of only 35% of bee species between sampling periods and similar results have been observed by other researchers (Williams et

Table 2. Honey bee preferences of flowering plant species with greater than 20 blooming stems. For ease of depiction, the top 10 preferred and 10 least preferred are shown. Honey bee abundance is the number of individual honey bees observed on each plant species among all sites, seasons, and years. Stem abundance is the total number of stems of each plant species among all sites, seasons, and years. Stem abundance rank is the plant species rank (1−*n*) based on stem abundance. Honey bee abundance rank is the ranked plant species (1−*n*) relative to the total number of honey bees observed. Honey bee preference rank is the difference between stem rank and honey bee abundance rank.

Plant common name	Honey bee abundance	Honey bee abundance rank	Stem abundance	Stem abundance rank	Honey bee preference rank
Common milkweed	37	3	190	17	14
Pennsylvania smartweed	79	1	314	14	13
Annual sunflower	4	10	54	21	11
Pitcher sage	5	9	118	19	10
Evening primrose	1	13	33	22	9
Stiff goldenrod	1	13	33	22	9
Common boneset	5	9	199	16	7
Golden Alexander	1	13	63	20	7
Butterfly milkweed	2	12	185	18	6
Canada goldenrod	25	5	760	10	5
Wild bergamot	45	2	5497	2	0
Tall thistle	1	13	388	13	0
Partridge pea	27	4	3521	3	−1
Yellow sweet clover	24	6	2254	5	−1
False sunflower	22	7	1978	6	−1
Red clover	9	8	1902	7	−1
Grey-headed coneflower	4	10	1187	8	−2
Foxglove beardtongue	2	12	1099	9	−3
Hairy vetch	3	11	3010	4	−7
Alfalfa	2	12	9325	1	−11

al. 2001).

In our study, bee species richness peaked in the mid-season (July), at the same time as plant richness and abundance, and was likely driven by phenological overlaps in the bee and forb communities. Previous studies have documented greater species turnover by season within specific ecological categories. For example, the rate of turnover for oligolectic species may be higher than generalist species between seasons due to their phenological overlap with host resources. By sampling through a seasonal gradient, we were able to encompass the diversity and turnover in bee community composition among the surveyed habitats through time (Table 1, Oertli et al. 2005).

During our surveys, we encountered several taxa of conservation concern. We collected a single female *Megachile rugifrons* (on Rattlesnake master) which is a rare bee species with

Table 3[1]. Classification and status of observed and collected bees by life history category. For species richness, each category totals 73 species, and percent total is 100%.

Category	Classification	Species richness	Percent total richness
Family	Andrenidae	10	13.7
	Apidae	29	39.7
	Colletidae	3	4.1
	Halictidae	22	30.1
	Megachilidae	9	12.3
Nesting	Ground	50	68.5
	Stem	6	8.2
	Cavity	8	11.0
	Domesticated	1	1.4
	Parasitic	6	8.2
	Rotting Wood	2	2.7
Sociality	Solitary	51	69.9
	Gregarious	1	1.4
	Social	10	13.7
	Eusocial	5	6.8
	Socially polymorphic	3	4.1
	Facultative	3	4.1
Lecty	Oligolectic	10	13.7
	Polylectic	57	78.1
	Parasitic	6	8.2
[1]Conservation Status	Status Secure (G4, G5)	33	45.2
	Not Recorded (GNR)	36	49.3
	Status Not Secure (G2, G3)	3	4.1
	Exotic	1	1.4

[1] G2: Imperiled globally, G3: Vulnerable globally, G4: Apparently secure globally, G5: Secure globally, GNR: Global status unknown.

declining populations known previously (in Nebraska) only from two confirmed records: one from Cedar Point Biological Station in 1988 and one from Mahoney State Park in 2011 (Ascher and Pickering 2020). Further, *M. rugifrons* is known only from prairie remnants and conservation lands, highlighting the importance of human-designed and implemented pollinator habitats like those examined in our study in supporting rare and declining bee species. Two species of *Bombus*, *B. fraternus* (Hatfield et al. 2014) and *B. pensylvanicus* (Hatfield et al. 2015), collected in our study are listed as endangered or vulnerable, respectively, under the IUCN Red List criteria (IUCN 2023) but currently have no federal protections and were collected among several sites, seasons, and on various plant species (SI Tables 2 and 3).

Another important finding in our study was that often the most abundant forbs, as determined via total stem counts, were commonly least preferred by bees. This mismatch is highlighted in the examples of Alfalfa and Partridge pea which ranked 1st and 3rd by total stem abundance among all plant species observed yet ranked as two of the least preferred species (Tables 2 and 3) by both honey bees and wild bees. Both species were commonly included in the seeding mixes among our study sites and they undoubtedly provide season-long food resources for bees, have climate-hardy growth habits, and economical seed costs. However, they were not preferred by either wild bees or honey bees. Previous studies have documented similar trends, finding that alternative sources of pollen and nectar may limit bee visitation (Bohart 1957, 1958) and ultimately impact indices of bee preference like the one used in this study (Pizante et al. 2023). For example, Bohart (1958) found that only when competing pollen sources are nearly eliminated over a large area is the number of bees foraging on Alfalfa noticeably increased. Related, some plants deemed “unpreferred” (e.g. Alfalfa, vetches, clovers) in our study may primarily be so due to their high flowering stem abundances, i.e. by calculation they are not preferred even though many bees were observed on them and, en masse, they provide substantial food resources for bee communities living among working lands. We emphasize caution in using the preference ranks found in Tables 2 and 3 as generalizable because bee preferences are context-dependent and there are other approaches to determining preference (Pizante et al. 2023).

Interestingly, Common milkweed was the most preferred plant species by honey bees and was preferred by honey bees more than wild bees (Tables 2 and 3). In addition to honey bee visitation, we observed nine distinct wild bee species on common milkweed including some relatively uncommon species such as *Anthophora bomboides* Kirby (Bumblebee-like digger bee) and *Nomia nortoni* Cresson (Norton’s alkali bee). Although milkweed does not serve as a pollen source for bees due to the structure of the pollinia, it is a significant source of nectar (Southwick 1983; Theiss et al. 2007).

We saw strong differential landscape use among honey bees and wild bees, which supports findings from previous studies (Otto et al. 2021, Rollin et al. 2013, Simanonok et al. 2021). There was relatively minimal overlap between honey bee and wild bee plant utilization throughout the growing season (Figures 4-6). In the early season, Common milkweed and Yellow sweet clover were important targets for honey bees, while Foxglove beardtongue received significant visitation from wild bee species, including bumble bee queens. In the mid-season, Wild bergamot was highly visited by both honey bees and wild bees, boasting a high bee abundance and wild bee species richness in visitations during those times. In the late season, sunflower and goldenrod species provide significant resources to wild bees and to a lesser extent, honey bees, which were seen abundantly visiting Pennsylvania smartweed. These findings indicate there are opportunities for improving pollinator and conservation habitat seed mixes by understanding which forb species were most and least utilized by different bee groups, and which forb species may result in reduced overlap between potentially competing bee species throughout the season.

The main limitations we encountered in this study included, 1) the snapshot sampling periods (i.e. one site visit per season), and 2) the narrowed sampling range (June – September) to estimate peaks within the growing season. It is likely that some plant and bee species were missed spatially or temporally during the surveys. For example, some bees within the region, e.g. *Andrena* spp., become active and then dormant prior to the initiation of our sampling each spring. These species are tightly aligned with the phenology of their host species, especially blooms of woody trees and shrubs (e.g. *Salix* spp., *Acer* spp., and *Malus* spp.). Further, our active collection methods may have resulted in missed bees during collection periods due to, 1) scaring them away while searching transects, and 2) visually missing bees, especially those that are cryptic in coloration or small in size.

Loss of high-quality habitat due to agricultural intensification is a leading cause of bee declines globally (Potts et al. 2010; Zattara and Aizen 2021). In this study we documented seasonal bee communities within established pollinator habitats among an agriculturally dominant landscape. Fluctuations in bee richness and abundance across the growing season and years highlight the need to supply a species-rich community of foraging resources throughout the growing season. Effective habitat establishments requires a deep understanding of species requirements throughout their lifecycles and life histories. The range of species needs, even within a target group such as pollinators, is widely diverse. Therefore, further research is needed to understand areas of best fit for pollinator habitat restoration, species-specific needs and preferences, and management. Tailoring conservation goals and habitat programs to prioritize specific bees or to target plants preferred by managed (i.e. honey bees) or non-managed bee species may be a useful tactic for reaching both agricultural and conservation goals.

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